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RESEARCH ARTICLE

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Potential alien ranges of European plants will shrink in the future, but less so for already naturalized than for not yet naturalized species

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Abstract

Aims: The rapid increase in the number of species that have naturalized beyond their native range is among the most apparent features of the Anthropocene. How alien species will respond to other processes of future global changes is an emerging concern and remains poorly misunderstood. We therefore ask whether naturalized species will respond to climate and land use change differently than those species not yet naturalized anywhere in the world.

Location: Global.

Methods: We investigated future changes in the potential alien range of vascular plant species endemic to Europe that are either naturalized ($n = 272$) or not yet naturalized (1,213) outside of Europe. Potential ranges were estimated based on projections of species distribution models using 20 future climate-change scenarios. We mapped current and future global centres of naturalization risk. We also analysed expected changes in latitudinal, elevational and areal extent of species' potential alien ranges.

Results: We showed a large potential for more worldwide naturalizations of European plants currently and in the future. The centres of naturalization risk for naturalized and non-naturalized plants largely overlapped, and their location did not change much under projected future climates. Nevertheless, naturalized plants had their potential range shifting poleward over larger distances, whereas the non-naturalized ones had their potential elevational ranges shifting further upslope under the most severe climate change scenarios. As a result, climate and land use changes are predicted to shrink the potential alien range of European plants, but less so for already naturalized than for non-naturalized species.

Main conclusions: While currently non-naturalized plants originate frequently from mountain ranges or boreal and Mediterranean biomes in Europe, the naturalized ones usually occur at low elevations, close to human centres of activities. As the latter are expected to increase worldwide, this could explain why the potential alien range of already naturalized plants will shrink less.

KEYWORDS
Alien plant species, biological invasions, climate change, distributional range shift, interacting effect of global changes, land use change, macroecology, migration, non-analogue climate, species distribution model

1 | INTRODUCTION

Alien species (i.e., species introduced by humans to regions outside of their native range; Essl et al., 2018; Pyšek, Richardson, Rejmánek, et al., 2004) have become a significant component of global change in the Anthropocene (Mooney & Hobbs, 2000; Seebens et al., 2017). As alien species are often considered to be "passengers" of other human-induced changes (MacDougall & Turkington, 2005), their prevalence is expected to increase by land use intensification, which is altering disturbance regimes and resource availability (D'Antonio et al., 1999; Chytrý et al., 2012; Lembrechts et al., 2016). Similarly, climate change is altering native species distributions and community composition (Gottfried et al., 2012; Lenoir et al., 2020; Pearson et al., 2013), creating opportunities for alien species to establish or expand. Therefore, alien species' responses to land use and climate change may lead to new centres of biological invasions (Bellard et al., 2013; Dullinger et al., 2017), with the possibility for synergistic effects (Oliver & Morecroft, 2014).

Previous studies argued that global change would promote alien species by enabling population establishment and persistence, and offering new opportunities for introductions (Hellmann et al., 2008; Walther et al., 2009). Indeed, experimental studies indicate that many alien plants might take more advantage of increased CO_2 levels and temperatures than many native plants (Haeuser et al., 2017;

Liu et al., 2017). However, in a recent review of 71 publications covering 423 naturalized (i.e., alien species reproducing naturally in the recipient ecosystems) and invasive species (i.e., rapidly spreading alien species, which frequently alter the composition, structure and functioning of the recipient ecosystems), climate change was more frequently projected to contribute to a decrease in range size than an increase (Bellard et al., 2018). The underlying causes and whether this pattern remains the same when accounting for land use change are unknown.

Species that are already naturalized somewhere are also more likely to naturalize elsewhere (Daehler & Strong, 1993; Mayer et al., 2017; Pyšek et al., 2003). Nevertheless, the number of emerging naturalized species (i.e., species that had never before been recorded as naturalized) is also steadily increasing (Seebens et al., 2018). It was recently estimated that the global pool of candidate species for naturalized vascular plants is ~47,000 (Seebens et al., 2018), which is ~3.5 times larger than the current number of naturalized vascular plants (van Kleunen et al., 2019). Because species distribution models (SDMs) for alien species usually focus on those aliens that are already naturalized, and particularly those that are considered invasive, little is known about the potential future change in alien distributions when incorporating the pool of species not yet naturalized.

Different hypotheses predict that distributional patterns of naturalized and currently non-naturalized species will become either more distinct or more similar. First, the typically broad environmental tolerance of widespread naturalized and invasive species suggests that they may be less sensitive to climate change compared to currently non-naturalized species (Thuiller et al., 2005). Future changes in the potential alien ranges of naturalized species are thus expected to be of relatively smaller magnitude than those of currently non-naturalized species. Second, given their close associations with anthropogenic habitats (MacDougall & Turkington, 2005), naturalized species are expected to persist in currently occupied areas while also colonizing newly suitable areas in conjunction with land use changes. Therefore, the potential alien ranges of naturalized species are expected to expand while those of currently non-naturalized species are expected to shrink. Third, a significant proportion of species could originate from climates with no or an increasingly scarce future analogue (Williams & Jackson, 2007), leading to a decrease in their future potential alien range, which would also apply equally to naturalized and non-naturalized species. For instance, this might be the case for plant species native to the Mediterranean biome, which is predicted to become increasingly restricted (Dullinger et al., 2017). As these hypotheses predict different patterns, comparisons of expected shifts in potential alien ranges between naturalized and currently non-naturalized species of the same continent of origin may shed light on the processes that drive future changes in naturalized species distributions.

Europe is the second most important donor continent of naturalized alien plant species after Asia, but, relative to the number of native species, the European flora has by far the greatest proportion of species naturalizing on other continents (Kalusová et al., 2017; van Kleunen et al., 2015). Of the ~14,000 vascular plant species native to Europe, 3,383 are known to be naturalized somewhere in the world, which is three times more than expected from the global average (van Kleunen et al., 2015). Furthermore, five of the ten most widely naturalized plant species globally are native to Europe (Pyšek et al., 2017). As a result, the European flora provides an excellent study system to determine whether future climate and land use changes will promote or limit the spread of naturalized species and, if so, where.

To estimate the actual and future (years 2061–2080) potential ranges of both naturalized and not yet naturalized plants outside Europe, we used ensemble species-distribution models for 1,485 European endemic plant species considering both climate and land use data. Specifically, we investigated: (1) how areas with high potential richness in alien plants native to Europe are predicted to change in the course of climate and land use changes and (2) whether changes in the potential alien distribution of species naturalized and not yet naturalized outside Europe will differ in latitude, elevation and range size.

2 | METHODS

2.1 | Modelling the potential alien ranges of plant species under current climatic and land use conditions

2.1.1 | Species selection

Many plant species native to Europe are also native to other continents such as Asia and Africa, for which there are much fewer data on species occurrences in global repositories (Meyer et al., 2016). Therefore, we focused exclusively on vascular plant species endemic to Europe, as this allows us to better capture the full realized niche of the species in their native continent (Gallien et al., 2010). Here, "Europe" is used in a geographical sense and defined as bordered by the Arctic Ocean to the north, the Atlantic Ocean to the west (the Macaronesian archipelagos were excluded), the Ural Mountains and the Caspian Sea to the east and the Lesser Caucasus and the Mediterranean Sea to the south (Mediterranean islands included, Anatolia excluded; Supplementary Information Figure S1).

The most recent version of the database "Endemic vascular plants in Europe" (EvaplantE; Hobohm, 2014), containing >6,200 endemic plant taxa, was used here as a baseline for species selection. Scientific names were standardized based on The Plant List (http://www.theplantlist.org/). This taxonomic standardization was done with the R package "Taxonstand" (Cayuela et al., 2017). Infraspecific taxa were excluded from the list, resulting in 4,985 species.

The naturalization status of the European endemic flora was obtained from the "Global Naturalized Alien Flora" (GloNAF) database, version 1.2, a recently compiled database of ~14,000 naturalized alien plant species (van Kleunen et al., 2019). A total of 407 European endemic species are recorded in GloNAF as naturalized somewhere in the world, and 4,578 European endemic species are not recorded

in GloNAF as naturalized, irrespective of whether they have been introduced elsewhere or not.

2.1.2 | Compilation of occurrence records

The native range of European endemics sometimes reflects biogeographical barriers (e.g., mountain ranges, seas) rather than true climatic limitations. In such cases, considering native occurrences only would lead to climatic niche truncation and an underestimation of the potential alien range of the species in our dataset (cf. Feeley, 2015). Moreover, a problem with developing models by using observations from the native range only is that the ecological requirements of the species might have changed during the naturalization process, thus violating the assumption of niche conservatism (Pearman et al., 2008). To reduce these problems, we considered native occurrences in conjunction with naturalized occurrences in Europe. This allowed us to get a more complete picture of species environmental niches and, therefore, to build more transferable models with more meaningful predictions where the species could potentially occur (Gallien et al., 2010). This pooled approach has been shown to be particularly relevant to improve predictions of the future extent of naturalizations (Broennimann & Guisan, 2008).

To comprehensively compile the distribution of our studied set of endemic species in their native continent, we combined occurrence data in Europe from five sources. The first source was the "Global Biodiversity Information Facility" (GBIF), one of the largest and most widely used biodiversity databases (https://www.gbif.org/ accessed on 17 October 2018). Currently, GBIF provides access to more than 600,000 distributional records for European endemic plant species. Although GBIF offers a relatively good coverage of Europe, it remains subject to taxonomic and geographical biases, gaps and uncertainties (see Meyer et al., 2016). Records of European endemic plants deemed erroneous were discarded (Table S1). All occurrences from GBIF were downloaded using the R package "rgbif" (Chamberlain et al., 2019). The second source was the "EU-Forest" dataset, providing information on European tree species distribution, including more than half a million occurrences at a 1-km (~ 50 arcsec at 50° latitude) resolution (Mauri et al., 2017). The third source we used was the "European Vegetation Archive" (EVA), which assembles observations from more than one million vegetation plots across Europe (Chytrý et al., 2016). Unlike GBIF and EU-Forest data, the EVA database includes comprehensive local plant community inventories (i.e., relevés) for various life-forms. This database remains geographically imbalanced with more data in Western, Central and Southern Europe than in Northern and Eastern Europe, but it significantly complements GBIF data, which are sparser in Southern and Eastern-Central Europe. The fourth source was the digital version of the Atlas Florae Europaeae offering gridded maps. The main limitations of this dataset is its coarse spatial resolution (cells of 50-km resolution, i.e., ~ 0.70° at 50° latitude) and restricted taxonomic coverage (~30% of the European flora; https://www.luomus.fi/en/publishing-atlas-florae-europaeae). The fifth source was the "Plant Functional Diversity of Grasslands" network (DIVGRASS), combining data on plant diversity across ~70,000 vegetation plots in French permanent grasslands (Violle et al., 2015). This dataset did not cover all of Europe but was included to maximize regional information on native distributions.

When several occurrences from these different sources were duplicated on the same 0.42° × 0.42° grid cell (~47 km at the equator, 30 km at 50° latitude), only one record was kept to avoid pseudoreplication. After removing duplicate records, species with fewer than 10 occurrences were not further considered as the resulting SDM might be insufficiently accurate (van Proosdij et al., 2016). In a preliminary analysis, we assessed whether SDM performance increased with increasing sample sizes and found no such relationships, suggesting that the minimum number of records required to obtain reliable SDMs (asymptote) was reached (Figure S2). The final dataset comprised 104,313 occurrences for 1,485 European endemic species, that is, 70 occurrences per species on average with a maximum of 957 occurrences for *Achillea ptarmica*. A total of 272 of those species (18%) were reported to be naturalized outside Europe, and the remaining 1,213 species (82%) were considered non-naturalized outside Europe, irrespective of whether or not they were introduced outside Europe (Table S2; van Kleunen et al., 2019). Almost half of species naturalized outside Europe were also naturalized in Europe (127 species; 47%). One sixth (17%) of the occurrences for these species were located in European countries where the species are considered as alien and the rest of available occurrences (83%) were found in countries where the species are considered as native. However, the exact proportion of alien occurrences is likely to be higher as a significant number of species are native in part of a country (e.g., *Pulmonaria officinalis* in Northern Italy) and alien in another part (e.g., *Pulmonaria officinalis* in Southern Italy: Figure S1), but this proportion is difficult to assess at finer scale given the limitation that most European plant databases use countries as basic geographical unit.

2.1.3 | Environmental variables

We selected six environmental predictors related to climate, soil physico-chemical properties and land use, commonly considered to shape the spatial distribution of plants (Gurevitch et al., 2006). Annual mean temperature (°C), annual sum of precipitation (mm) and precipitation seasonality representing the period 1979–2013 were extracted from the CHELSA climate model at a 30 arcsec resolution (Karger et al., 2017). Organic carbon content (g per kg) and soil pH in the first 15 cm of topsoil were extracted at a 1-km resolution from the global gridded soil information database SoilGrids (Hengl et al., 2014). The proportion of primary land cover (land with natural vegetation that has not been subject to human activity since 1,500) averaged over the period 1979–2013 in each 0.42° resolution grid cell (variable "gothr") based on the Harmonized Global Land Use dataset was also used (Chini et al., 2014). Environmental variables were aggregated at a spatial resolution of 0.42° × 0.42° to approach the cell

size of the occurrence records with the coarsest resolution (i.e., the Atlas Florae Europaeae). Pairwise correlations between the six predictor variables did not exceed the threshold of $|r| = 0.70$ beyond which collinearity begins to severely distort model estimations and subsequent predictions (Figure S3; Dormann et al., 2013). However, these variables reflecting trends in average climate conditions were significantly correlated with climate extremes to which plants are recognized to be highly responsive (Zimmermann et al., 2009).

2.1.4 | Species distribution modelling

The potential distribution of 1,485 European endemic plant species was predicted by estimating environmental similarity to the sites of occurrence in Europe. To increase robustness of the predictions, we used six methods to generate SDMs: generalized additive models, generalized linear models (GLMs), generalized boosting trees, maximum entropy, multivariate adaptive regression splines and random forests. All of these methods require both presences and either true absences or pseudo-absences (a random subset of the available environmental conditions in the area, i.e., Europe in our case), whose selection can significantly affect predictions (Barbet-Massin et al., 2012). We performed a preliminary analysis to identify the most appropriate set of pseudo-absences for each SDM method (Appendix S1). We evaluated the predictive performance of each SDM using a repeated split sampling approach in which SDMs were calibrated over 75% of the data and evaluated over the remaining 25%. This procedure was repeated 10 times. The evaluation was performed by measuring the area under the receiver operating characteristic (ROC) curve (AUC) (Fielding & Bell, 1997) and the true skill statistic (TSS) (Allouche et al., 2006). ROC curves were constructed by using all possible thresholds to classify the scores into confusion matrices, obtaining sensitivity and specificity for each matrix, and then plotting sensitivity against the corresponding proportion of false positives. AUC values range from 0 to 1, where 1 indicates a perfect fit, and 0.5 indicates that predictions from the SDM do not differ from random, and 0 means the SDM is always incorrect. TSS is a threshold-dependent metric calculated as: sensitivity + specificity − 1. Continuous model predictions were transformed into binary ones by selecting the threshold maximizing TSS to ensure the most accurate predictions as it is based on both sensitivity and specificity (Jiménez-Valverde and Lobo 2007). TSS ranges from −1 to 1, where 1 indicates perfect agreement, 0 indicates a random prediction and negative values indicate that predictions perform worse than random.

Results of the different SDM methods were aggregated into a single consensus projection (i.e., map) to reduce uncertainties associated with each technique (Araújo & New, 2007). This approach would produce more robust predictions of plant invasion risks than those of individual SDMs (Guan et al., 2020; Stohlgren et al., 2010). To ensure the quality of the ensemble SDMs, we only kept the projections for which the accuracy estimated by AUC and TSS were higher than 0.8 and 0.6, respectively, and assembled the selected SDMs using a committee-average approach with a weight proportional to their TSS evaluation (Marmion et al., 2009). The entire species distribution modelling process was performed within the "biomod2" R platform (Thuiller et al., 2009), and is synthesized following the standard protocol ODMAP (Overview, Data, Model, Assessment and Prediction; Zurell et al., 2020) in Appendix S2.

2.2 | Modelling the potential alien ranges of plant species under future climatic conditions

To model the potential spread of the European endemic flora outside of Europe in the future, we used projections for the four representative concentration pathways (RCPs) of both climate and land cover data for the period 2061–2080. Because of the substantial climatic differences predicted by different general circulation models (GCMs; Knutti & Sedlacek, 2013), which result in concomitant differences in species range projections, simulations of future climate variables were based on five different GCMs: CCSM4, CESM1-CAM5, CSIRO-mk3-6-0, IPSL-CM5A-LR and MIROC5.

For each of the 20 RCP-GCM combinations, final binary consensus maps were stacked to estimate the number of species that would find suitable environmental conditions in each grid cell (Figure S4). As in Dullinger et al. (2017), we defined centres of naturalization risk as the top 10% of cells that provide a suitable climate and land use to the highest numbers of alien species endemic to Europe for which we built SDMs. To depict potential contraction or expansion of centres of naturalization risk, we also mapped these centres by applying the top 10% cut-off value determined under current conditions to the future climatic scenarios (also see Dullinger et al., 2017). These maps were computed for naturalized plants endemic to Europe (10% cut-off value = 50 species) and for currently non-naturalized European endemics (210).

Further, we evaluated whether predicted changes in the potential alien range of naturalized and non-naturalized European endemic plant species differ in: (1) the optimum (i.e., mean value) and breadth (i.e., standard deviation) of latitude (Hirzel et al., 2002); (2) the optimum and breadth of elevation derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model with an original resolution of 90 m aggregated at 0.42° × 0.42°; and (3) range size estimated in metric units using the angular to planar transformation performed by the *area* function of the "raster" R package (Hijmans et al., 2019). These variables were scaled to a mean of zero and a standard deviation of one to improve the interpretability of regression coefficients.

The latitude, elevation and size of species ranges are not completely independent (e.g., species with a larger potential alien range also tended to have a wider latitudinal breadth; $r = 0.43$). Therefore, explanatory variables were jointly compared using GLMs (with naturalization status as response variable) built for current conditions and each RCP-GCM combination. Moreover, certain taxonomic ranks were over-represented in our studied set of species (e.g., 153 species of the genus *Rubus* and 224 species of the family Rosaceae). Therefore, we controlled for between-species phylogenetic

TABLE 1 Results of the phylogenetically controlled generalized linear models testing whether the latitude, elevation and range size of the current realized ranges in Europe (i.e., based on collected occurrence records) and the current potential ranges outside of Europe (i.e., based on the predictions of species distribution models) relate to naturalization of species endemic to Europe

		Latitude optimum (°)			Latitude breadth (°)			Elevation optimum (m)			Elevation breadth (m)			Range size (in no. of occurrences and million km^2, respectively)		
	s2	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value
Realized range in Europe	0.99	0.12	1.25	.213	0.54	5.89	**.000**	−1.13	−6.18	**.000**	0.84	5.45	**.000**	0.41	4.28	**.000**
Potential range outside Europe	1.67	0.73	5.75	**.000**	0.32	3.26	**.001**	−0.38	−3.56	**.000**	−0.30	−1.28	.202	0.39	3.68	**.000**

Note: Explanatory variables were centred and standardized. *s2* denotes the strength of the phylogenetic signal, estimate (Est.) is the amount by which the log odds of naturalization status (0 = not yet naturalized, 1 = already naturalized) would increase if range characteristics were one standard deviation higher and *z* value is the logistic regression correlation coefficient. Values in bold indicate significant *p*-values (<.050).

distances in comparisons between naturalized and non-naturalized species (for details on the phylogeny used, see Supplementary Information Appendix S3). Phylogenetically controlled GLMs were performed using the *binaryPGLMM()* function of the R package "ape" (Paradis et al., 2020). In this function, *s2* is the scaling component of the variance in the model, where *s2* = 0 suggests no phylogenetic signal and a high *s2* value implies strong phylogenetic signal (Nakagawa & Schielzeth, 2013). Our GLMs had an *s2* parameter in the range 0.99–1.67, indicating a very strong phylogenetic signal (Tables 1 and 2; Table S3).

3 | RESULTS

Plant species endemic to Europe and naturalized outside Europe had significantly more occurrence records within Europe than European endemic plant species not yet naturalized elsewhere (Table 1). For example, nine of the ten most common species in European plant databases were naturalized outside of Europe. Occurrence records in Europe indicated that naturalized species occupy cooler, drier, more climatically stable and more disturbed sites with soils richer in organic C and more acidic than sites occupied by non-naturalized species (Supplementary Information Figure S5). The former were also more tolerant to variations in the six environmental variables selected for species distribution modelling than the latter (Figure S5). In their native European range, the collected occurrence records showed that naturalized species occurred at lower elevation and had a higher latitudinal and elevational breadth than non-naturalized species (Table 1). Still, the two groups had their current average climatic optimum at similar latitude (Table 1 and Figure S6). As observed in the native range, naturalized species were predicted to find suitable conditions outside of Europe at a lower elevation and in a wider range of latitudes than non-naturalized species (Table 1). However, in contrast to their occurrences in Europe, naturalized species had their climatic optimum more poleward than non-naturalized species outside their native European range, while naturalized and non-naturalized species had a similar potential elevational range (Table 1).

The six major centres of naturalization risk of plant species endemic to Europe are the southeast of North America, Central America, the Andes, the South American pampas, the Central African mountains, temperate Australia and New Zealand and eastern China, independently of whether or not these endemic species are currently naturalized elsewhere (Figure 1). Indeed, the global overlap in the areas identified as current or future centres of naturalization risks is very large between species endemic to Europe already naturalized outside Europe and those not yet naturalized elsewhere. This pattern remained largely the same under different scenarios of future climate and land use changes (Figure 1).

The size of the future potential alien range of European endemic plants already naturalized outside Europe was predicted to decrease both in absolute value (Figure S7) and relative to the present potential range outside Europe (Figure 2) in all but three RCP-GCM combinations (2.6-CESM1-CAM5, 8.5-CESM1-CAM5 and 8.5-MIROC5).

TABLE 2 Results of the phylogenetically controlled generalized linear models testing whether predicted changes in latitude, elevation and range size (in % to the present range) between the current (1979–2013) and future (2061–2080) potential alien ranges relate to naturalization of species endemic to Europe

			Change in latitude optimum (°)			Change in latitude breadth (°)			Change in elevation optimum (m)			Change in elevation breadth (m)			Change in range size (% to present)		
RCP	GCM	*s2*	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value	Est.	*z* value	*p*-Value
2.6	CCSM4	1.36	−0.01	−0.08	.935	−0.10	−0.81	.420	0.33	1.55	.122	−0.12	−0.57	.571	0.20	1.79	.074
"	CESM1-CAM5	1.33	0.14	1.20	.229	−0.17	−1.37	.170	0.21	1.34	.181	−0.02	−0.11	.910	0.27	2.51	**.012**
"	CSIRO-mk3-6-0	1.33	0.06	0.56	.579	−0.17	−1.52	.128	0.46	3.05	**.002**	−0.42	−2.63	**.009**	0.19	1.80	.072
"	IPSL-CM5A-LR	1.41	0.20	1.83	.067	−0.19	−3.00	.086	0.39	2.09	**.037**	−0.38	−2.22	**.027**	0.27	2.62	**.009**
"	MIROC5	1.33	0.18	1.59	.112	−0.20	−1.78	.075	0.21	1.30	.196	−0.18	−1.05	.293	0.29	2.75	**.006**
4.5	CCSM4	1.36	0.48	4.19	**.000**	−0.32	−2.78	**.006**	−0.03	−0.16	.873	0.02	0.12	.906	0.36	3.63	**.000**
"	CESM1-CAM5	1.27	0.59	5.47	**.000**	−0.12	−1.15	.251	−0.00	−0.02	.987	0.04	0.28	.779	0.19	1.97	**.048**
"	CSIRO-mk3-6-0	1.33	0.14	1.68	.094	−0.12	−1.30	.193	0.25	2.02	**.044**	−0.10	−0.97	.333	0.24	2.70	**.007**
"	IPSL-CM5A-LR	1.28	0.41	4.59	**.000**	−0.20	−2.02	**.043**	0.17	1.38	.168	−0.23	−2.11	**.035**	0.28	3.26	**.001**
"	MIROC5	1.28	0.38	3.90	**.000**	−0.16	−1.62	.105	−0.01	−0.10	.924	0.08	0.58	.562	0.32	3.43	**.001**
6.0	CCSM4	1.33	0.34	3.19	**.001**	−0.30	−2.66	**.008**	−0.06	−0.33	.740	0.04	0.19	.847	0.38	3.40	**.001**
"	CESM1-CAM5	1.35	0.44	4.48	**.000**	−0.18	−1.54	.123	−0.16	−1.08	.282	0.12	0.76	.448	0.21	1.96	.050
"	CSIRO-mk3-6-0	1.37	0.26	2.63	**.009**	−0.27	−2.55	**.011**	0.02	0.14	.890	0.01	0.06	.954	0.33	3.11	**.002**
"	IPSL-CM5A-LR	1.30	0.37	4.19	**.000**	−0.34	−3.05	**.002**	0.03	0.21	.835	−0.20	−1.43	.154	0.37	3.59	**.000**
"	MIROC5	1.28	0.42	4.35	**.000**	−0.24	−2.25	**.025**	−0.04	−0.29	.776	0.03	0.18	.860	0.32	3.19	**.001**
8.5	CCSM4	1.35	0.39	5.64	**.000**	0.01	0.13	.899	−0.17	−1.23	.220	−0.02	−0.19	.852	0.10	1.22	.223
"	CESM1-CAM5	1.30	0.35	5.47	**.000**	0.03	0.41	.685	−0.24	−2.12	**.034**	0.13	1.12	.261	0.09	1.20	.232
"	CSIRO-mk3-6-0	1.44	0.24	3.94	**.000**	−0.01	−0.11	.913	−0.02	−0.16	.873	−0.00	−0.02	.982	0.21	2.68	**.007**
"	IPSL-CM5A-LR	1.31	0.35	6.40	**.000**	0.06	0.81	.419	−0.10	−0.91	.365	−0.12	−1.28	.200	0.08	1.19	.235
"	MIROC5	1.31	0.39	6.34	**.000**	0.06	0.75	.456	−0.06	−0.57	.572	−0.07	−0.57	.568	0.10	1.46	.145

Note: Explanatory variables were centred and standardized. *s2* denotes the strength of the phylogenetic signal, estimate (Est.) is the amount by which the log odds of naturalization status (0 = not yet naturalized, 1 = already naturalized) would increase if range characteristics were standard deviation higher and *z* value is the logistic regression correlation coefficient. Values in bold indicate significant *p*-values (<.050).

Abbreviations: GCM, general circulation models; RCP, representative concentration pathways

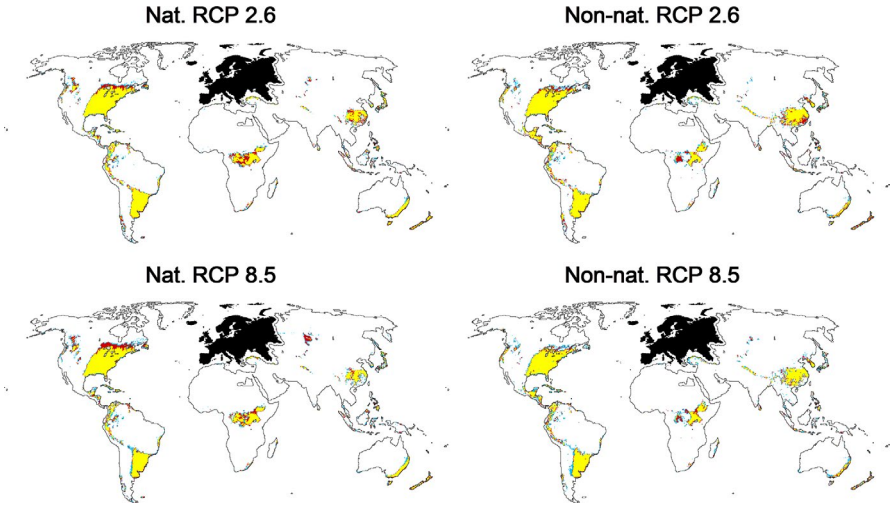

FIGURE 1 Potential centres of naturalization risk of plant species endemic to Europe that are naturalized somewhere in the world ("Nat."; left column) and currently non-naturalized ("Non-nat."; right column). Present hotspots are displayed in blue, future (2061–2080) hotpots in red and the overlap between both in yellow. These maps were obtained by stacking 272 naturalized species distribution models (SDMs) and 1,213 non-naturalized SDMs, and then selecting the 10% of cells that provide a suitable climate and land-use to the highest numbers of species in each stack. This top 10% cut-off value was determined under current conditions (50 naturalized species and 210 non-naturalized species) and applied to the most extreme climate representative concentration pathways (RCPs 2.6 and 8.5). Potential species richness of each RCP was obtained by calculating the median value of five global circulation models (CCSM4, CESM1-CAM5, CSIRO-mk3-6-0, IPSL-CM5A-LR and MIROC5)

The same applies to European endemic plants not yet naturalized outside Europe for all scenarios. Nevertheless, the future potential range size for naturalized species decreased significantly less (mean change for all RCP-GCM combinations = −0.3 million km^2) than for non-naturalized species (−0.5 million km^2; Tables 2 and S3).

Naturalized and non-naturalized species were both projected to have wider potential latitudinal ranges in the future than at present, but less so for naturalized species than for non-naturalized species (Table 2). However, the potential alien ranges of naturalized species are expected to move further poleward (mean shift for all RCP-GCM combinations = +1.5° latitude over 70–80 years) than those of currently non-naturalized species (+1.0° latitude), and this was more pronounced for the most severe climate change scenarios (Tables 2 and Table S3). Potential alien ranges are expected to move to higher elevations too. However, while the potential alien ranges of naturalized species will move further upslope than those of currently non-naturalized species under the most moderate climate change scenarios (RCP 2.6; mean shift = +61 and +54 m, respectively), this was not true, and even reversed, for the most severe climate change scenarios (RCP 8.5; +78.5 and +107 m, respectively; Tables 2 and S3). Generally, the studied species will be able to potentially occupy a broader range of elevations than at present, and this tendency was significantly greater for the non-naturalized species in many RCP-GCM combinations (Tables 2 and Table S3).

4 | DISCUSSION

Our results indicate that European endemic plants that have naturalized elsewhere in the world are more widespread and occur at lower elevations in Europe than the ones that have not naturalized elsewhere. In line with the higher elevation distributions of the non-naturalized species within Europe, their projected ranges outside Europe also included higher elevations than for species that have become naturalized. Non-naturalized species are more likely to be habitat specialists, being more often associated with seasonal, less productive or natural conditions in Europe than naturalized species. However, the two groups do not differ in elevational breadth of their potential alien range outside Europe. The non-naturalized species are also projected to occur at more equatorial latitudes and to have a narrower latitudinal breadth than naturalized species outside of Europe. Overall, our results indicate that the naturalized and non-naturalized endemic European plants differ in distributional characteristics in their native range as well as in the projected potential alien distributions outside of Europe.

We identified six global centres where many plant species endemic to Europe would be able to naturalize (Figure 1). These potential centres were similar for naturalized and non-naturalized plants, and their locations will not change much under projected future climates. Nevertheless, our modelling approach indicates that naturalized species will have their potential alien range shifting poleward over larger distances than currently non-naturalized species, whereas the non-naturalized ones will have their potential elevational ranges shifting further upslope than the ones from the naturalized species, at least under the most extreme RCP scenario (Table 2; Table S3). Overall, climate and land use changes are expected to shrink the potential alien ranges of European endemic plants outside Europe, but less so for already naturalized than for currently non-naturalized species (Table 2; Table S3). Nevertheless,

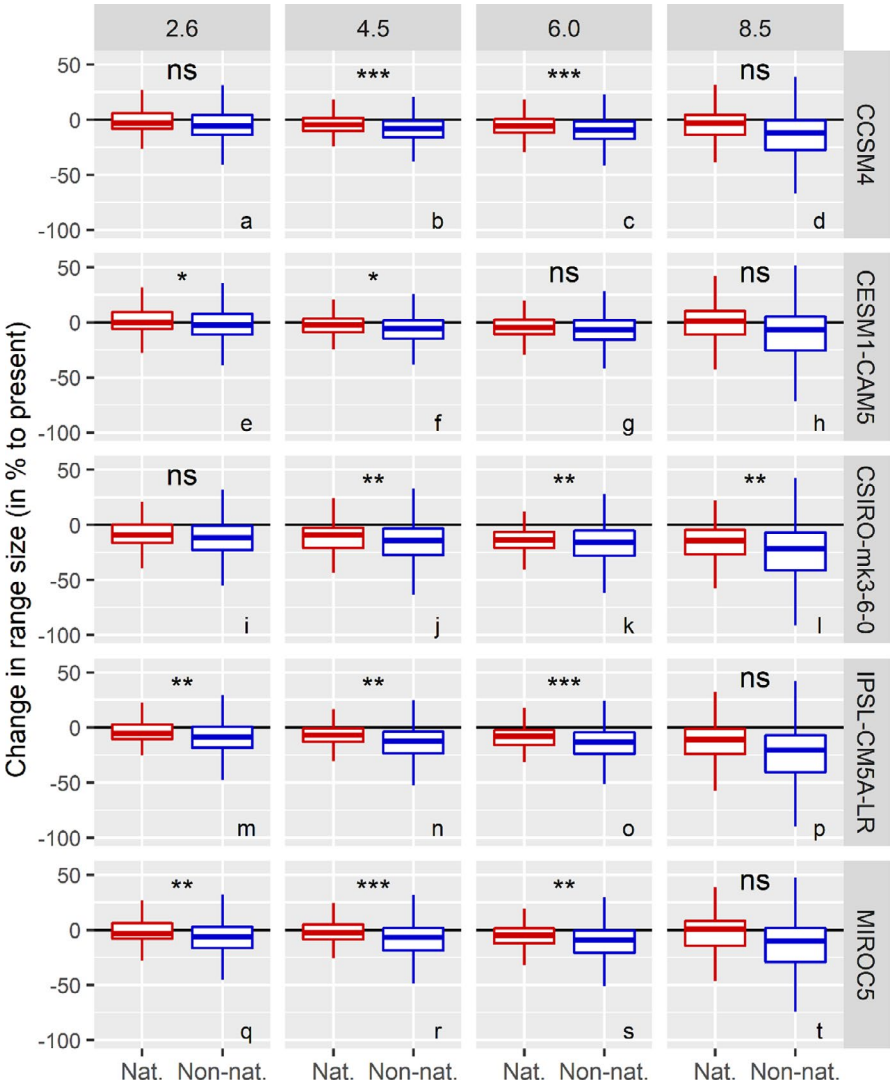

FIGURE 2 Predicted change in potential range size outside Europe (in % to the present range) of European endemic plants naturalized outside Europe ("Nat."; red) and European endemic plants not naturalized outside Europe ("Non-nat."; blue) for 2061–2080 according to different combinations of representative concentration pathways (RCPs, columns) and global circulation models (GCMs, rows). Comparisons have been performed using phylogenetically controlled generalized linear models. ns indicates *p*-Value >.05, *.05 > *p*-Value ≥ .01, **.01 > *p*-Value ≥ .001 and ****p*-Value < .001. Boxplots depict the median (heavy horizontal line), the quartiles (lower and upper edges of the box) and the minimum and maximum values excluding outliers (vertical whiskers)

our study shows that many European species will have the potential to establish in regions where they currently do not occur.

Like many other studies (Pyšek et al., 2009; Rejmánek, 1996), we found that species that are more widespread in their native range are more likely to naturalize elsewhere (Table 1). One possible explanation is that species that are more widespread in their native ranges have a larger environmental niche breadth (Figure S5), and also that they are less dependent on obligate mutualisms (Pyšek et al., 2019). Hence, ubiquitous and thus more frequently recorded species are commonly better invaders (Thuiller et al., 2012). This is also supported by other studies on naturalization success of European species in North America, where one of the strongest predictors was species niche breadth in the native range (Kalusová et al., 2017; Pyšek et al., 2015). Other potential explanations include that naturalized species are better dispersers than non-naturalized species, and that species that are common in their native range are more likely to have been picked up from the native range and widely introduced (van Kleunen et al., 2007; Novoa et al., 2016; Pyšek et al., 2004). The fact that many European endemic species have failed to naturalize, although many of them would have suitable environments outside Europe, could thus reflect that they were introduced less widely or not at all. A major pathway for the introduction of alien plants is their cultivation for ornamental and other economic value such as for animal fodder and medicines (van Kleunen et al., 2020). Indeed, we found that the percentage of ornamental (30.2%) and other economic plants (19.1%) among naturalized European endemics is much higher than among European endemics that have not yet become naturalized (4.3% and 2.4%, Pouteau, Thuiller, et al., 2021). Ongoing globalization will continue to result in species introductions, so it is likely that more of the currently non-naturalized species will be introduced elsewhere, and could naturalize.

Surprisingly, although naturalized and non-naturalized species occur on average at similar latitudes in their native European range, the projected potential latitudinal optima differed significantly between both groups (Table 1). Possibly, this reflects that although many naturalized species occur at temperate mid-latitudes in Europe, many non-naturalized species occur at high (subpolar climate) and low (Mediterranean climate) latitudes (Figure S6). Therefore, the averaged latitudinal optima within Europe of both groups largely overlap.

The fact that naturalized species occur more frequently in less natural habitats than currently non-naturalized species (Figure S5g), and that the former have their current elevational optima in Europe at lower elevations (Table 1), where human populations are denser, suggests that they have been picked up and introduced (intentionally or unintentionally) outside of Europe more frequently (Dostál et al., 2012; Kalusová et al., 2017; Prinzing et al., 2002). Indeed, van Kleunen et al. (2007) found that southern African Iridaceae were more likely to be used in international horticulture when they came from lower elevations. A similar idea would be that species that succeeded to naturalize are likely to benefit from anthropogenic activities (Alexander et al., 2016; MacDougall & Turkington, 2005), which are more intense and widespread at low elevations, while other species might have found refugia in the smaller high elevation habitats. Another possible explanation would be that both species groups have been picked up with the same frequency but, as non-naturalized species are more likely to be habitat specialists (i.e., with a narrower niche breadth; Figure S5), they might be less likely to be introduced to habitats with suitable conditions.

Considering that naturalized species are associated with anthropogenic habitats and that these habitats are expected to expand poleward (Figure S8), it is not surprising that the potential alien range of naturalized species is expected to shift poleward in latitude over larger distances than that of currently non-naturalized species (Table 2 and Table S3). However, given that non-naturalized species currently occur at higher elevations in Europe (Table 1), their future potential alien range would have been expected to be distributed at higher elevations than that of naturalized species, which was only true under the most pessimistic RCP (Table 2 and Table S3). Indeed, unlike the relationship between elevation and temperature, the relationship between elevation and precipitation can be idiosyncratic (Basist et al., 1994), so that precipitation changes should not be expected to cause coordinated directional shifts in species elevations (Lenoir et al., 2010; Stephenson and Das, 2011; Crimmins et al., 2011). Moreover, there are important between-GCM discrepancies in future precipitation patterns (e.g., on islands as pointed out by Harter et al., 2015), resulting in different responses of species distributions to climate change. As a result, predicted future potential alien ranges would be spatially patchy and highly uncertain (Breshears et al., 2011).

Overall, our findings show that the size of the future suitable alien range of European plant species that have become naturalized is more often expected to decrease than increase. This confirms the tendency for a decrease in suitable range sizes for invasive organisms with future climate and land use change found in a systematic review by Bellard et al. (2018). By contrast, Haeuser et al. (2018) found that in Europe, the potential ranges of alien species will more often increase than decrease, although the difference was minimal. They also found that this applied to both naturalized and currently non-naturalized alien cultivated species, whereas we found that the future potential alien range will be smaller to a greater extent for currently non-naturalized European endemic plant species than for naturalized ones. Because both naturalized and currently non-naturalized species were predicted to shift poleward but naturalized species are predicted to shift further, this difference in range contraction cannot be directly attributed to the decrease in the available area as latitude increases (as a consequence of the spherical shape of the Earth). Furthermore, as we found inconsistent shifts along the elevation gradient according to RCP-GCM combinations between naturalized and currently non-naturalized species, this pattern cannot be attributed to an elevational shift either (because the rough conical shape of mountains provides smaller potential areas for species as elevation increases, but see Elsen and Tingley 2015). A possible explanation could be that naturalized species, which are frequently associated with anthropogenic habitats, such as arable land or ruderal places (Kalusová et al., 2017; Figure S5g), are taking advantage of land conversion. However, this would imply that differences between naturalized and currently non-naturalized species (i.e., the estimates) become larger when scenarios become increasingly pessimistic, but our data did not support this hypothesis (Table 2 and Table S3).

The apparent decrease in potential alien range size of naturalized and currently non-naturalized species may at least in part be driven by suitable climate and land use conditions in the future not aligned with suitable soil conditions. The heterogeneous changes in precipitation in conjunction with the relatively linear change in temperature and the expansion of anthropogenic encroachments over a mosaic of soils may lead to novel environmental combinations in the future (Williams & Jackson, 2007). Yet, SDMs cannot forecast how species will respond to non-analogue situations (Bellard et al., 2018; Fitzpatrick & Hargrove, 2009; Heikkinen et al., 2006). This could explain why both naturalized and currently non-naturalized species are projected to experience a decrease in the size of their potential range according to our current knowledge.

A remaining question is why the potential alien range of currently non-naturalized species is projected to shrink more significantly than that of naturalized species. We showed that a key ecological difference between the two groups is that naturalized species favour anthropogenic habitats located at low elevations, while currently non-naturalized species occupy higher elevation and non-temperate (i.e., boreal-arctic or Mediterranean) latitudes in Europe (Figure S6). Yet, the surface area occupied by anthropogenic habitats will likely increase in the future (Figure S8), while novel climate combinations are recognized to typically coincide with areas of boreal-arctic and Mediterranean climate and high elevations (Ackerly et al., 2010; Dullinger et al., 2017; Forester et al., 2013; Stralberg et al., 2009). Thus, although there are substantial uncertainties about whether or not the potential alien range of naturalized and currently non-naturalized species will decline in response to climate and land use changes, our results show that naturalized species will be less exposed to potentially unsuitable novel climatic conditions than currently non-naturalized species.

In conclusion, our results suggest that vascular plant species endemic to Europe already naturalized elsewhere in the world are likely to benefit from future climate and land use change relative to vascular plant species endemic to Europe that have not successfully

naturalized yet, even if these changes overall will put negative pressure on most species. We showed that species already naturalized outside Europe occur more in the lowlands of Europe, closer to human populations, than species currently not naturalized elsewhere. As they currently have different distributions in their native continent, it makes sense that they will also have different future ranges in their naturalized range outside Europe. A key difference could be their exposure to non-analogue future climates, with currently non-naturalized species probably facing more frequently uncertain novel climates than naturalized species. This could explain why the potential alien ranges of currently non-naturalized species are expected to be more impacted by climate and land use change than those of naturalized alien species. Importantly, as most European endemic species have not yet filled their current potential alien ranges, we can still expect an increase in naturalization of European plants overall, and especially in the six global centres of naturalization risk, even when the future potential ranges will decrease.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13378.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study (naturalized plant inventories, occurrence records and environmental variables) came from openly accessible repositories cited in the manuscript (for details on the EVA database, see http://euroveg.org/eva-database-obtaining-data). All present and future habitat suitability raster files are available from the Dryad Digital Repository: https://datadryad.org/stash/dataset/doi:10.5061/dryad.qv9s4mwf3 (Pouteau, Biurrun, et al., 2021).

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BIOSKETCH

Robin Pouteau is a plant ecologist at IRD (French Research Institute for Sustainable Development) with a strong focus on the impact of biological invasions on biodiversity. This project is the result of a collaboration with two consortia of international researchers working on plant inventories: Global Naturalized Alien Flora (GloNAF) and European Vegetation Archive (EVA).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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